THE EMPETRACEAE AND DIAPENSIACEAE OF THE SOUTHEASTERN UNITED STATES

C. E. Wood, Jr. and R. B. Channell

The studies of Empetraceae and Diapensiaceae, two small families of both biosystematic and phylogenetic interest considered below, are part of a generic flora which is in preparation for the southeastern United States.[1] The genera of these families provide examples on a different level of complexity from those of nine families of Ranalian affinities, the treatments of which have been published previously (Jour. Arnold Arb. 39: 296–346. 1958; 40: 94–112. 1959). Further examples of the diversity of the plants of this area and of the problems which they present will be published as space permits in order that some of this material may be

[1] Preliminary to a manual of the species of seed plants of this area, generic treatments of this type are intended to call attention to problems of various kinds which will require the talents of all available workers before it will be possible to understand thoroughly the plants of this large area; to bring together a large part of the information available concerning the genera which occur there; to focus attention where possible on the biosystematic aspects of each group; and to examine and clarify the confused generic lines so often found among groups of plants in the southeastern United States. Although to some the approach from the generic level may seem a roundabout one, we are confident that, by bringing together in one place information of the kind presented in the treatments below, the widest interests of taxonomy and taxonomists will be served in both research and teaching and that the ultimate goal of an understanding of the plants of the area will be reached more quickly through this approach than through the traditional one.

While one may speak of "alpha" and "omega" taxonomy and insist that one precede the other, in times such as the present with the ever increasing destruction of the natural areas of the earth — a process all too evident in the southeastern United States — it is important as never before that taxonomic problems be approached simultaneously on all levels, from the alpha to the omega, and from all directions, and that the taxonomist have the knowledge and viewpoint to do this. It is not sufficient to say "Collect now — study later." The very items the monographer or careful student of evolution may need to know are the ones which may easily be overlooked (and often are) by the well-meaning but uninformed collector. Provided with a guide to some of the critical features which need observation, with some idea as to the basis of the taxonomic complexities of a group, or with a knowledge of the gaps in the information available concerning a group of plants, a worker is in a much more favorable position to obtain critical information in the field, and to look at plants with an awareness which is lacking among those whose aim is only to collect and identify. If taxonomy as a science is to command the respect of workers in other disciplines, if it is to be both analytic and synthetic, and if a modern flora of any area is to have a firm basis in an understanding of the plants involved, the approach must be one of understanding plants as living organisms and the information considered must come from all branches of botany and from all levels — from the alpha to the omega. Generic treatments of the kind presented here may serve the interests of workers on any of these levels. Certainly a number of taxonomic and phylogenetic, as well as morphological and biological, problems will be apparent to the thoughtful reader of the descriptions, notes and references which follow. — C. E. W.

made more immediately available to those interested in the plants of eastern North America.

The general scheme of these studies is outlined in the first paper of this series (see above). It should be pointed out again, however, that the southeastern United States as defined here is bounded by and includes North Carolina, Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within our area, any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals are the very useful ones of Lazella Schwarten and H. W. Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club 76: 277–300. 1958); and that references which we have not seen are marked by an asterisk. All of this work, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation.

The detailed drawings of the four genera are the careful work of Dorothy H. Marsh. We are indebted to H. L. Blomquist, of Duke University, and to R. K. Godfrey, of Florida State University, for their respective kindness in sending for study and use in illustration a large series of specimens of *Pyxidanthera brevifolia* and excellent fresh specimens of *Ceratiola* in fruit.

EMPETRACEAE (CROWBERRY FAMILY) [2]

A small family of evergreen shrubs of ericoid habit with numerous pulvinate leaves, inconspicuous apetalous flowers of few stamens and drupaceous fruits. Three genera of disjunct distribution and about eight species: *Empetrum* L., bicentric, with about four boreal species, primarily of arctic to subalpine distribution, and a single species in the subantarctic; *Corema* D. Don, with *C. Conradii* (Torrey) Torrey ex Loud., in widely separated areas from the Magdalen and Prince Edward islands and Nova Scotia to New Jersey, and *C. alba* (L.) D. Don in Portugal and the Azores; and the monotypic *Ceratiola* Michx. confined to our area.

The systematic position of the Empetraceae has been the subject of considerable controversy. The family has been variously allied with the Celastrales, Ericales and Sapindales. The erect ovule and ventral raphe have been considered to indicate affinities with the Sapindales. A natural group, it is perhaps best regarded as a reduced apetalous and polygamous or dioecious derivative of the Ericaceae. This view is supported by the embryological data of Samuelsson and is confirmed by the morphological studies of Hagerup. A whole series of well-marked embryological features characterizes the Ericales. These represent standard stages in Ericalean embryology and constitute a combination unknown in any other order. The Empetraceae show close correspondence in all respects. The embryol-

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ogy of the Celastrales and Sapindales differs in so many ways as to render any link with the Empetraceae obscure indeed. The 3-colporate pollen grains are united in tetrahedral tetrads as in Ericaceae.

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1. **Ceratiola** Michx. Fl. Bor.-Am. **2**: 221. 1803.

Dioecious shrubs of dry sand strands and sand hills, emitting a characteristic odor. Leaves linear-acicular, in "decussate" whorls, with a longitudinal groove on the lower surface, jointed at the base of the short petiole. Old stems roughened by petiolar sterigmata. Flowers axillary, sessile, hypogynous, the perianth consisting of 5–6 bracts and sepals. Male flowers of 2 exserted stamens, the 2-loculed anthers longitudinally dehiscent; pollen in tetrads. Female flowers with a single pistil, the 3–4 exserted stigmas divergent, flabellate-incised-pinnatifid, united into the single style arising from the summit of the ovoid, 2-locular ovary. Fruit small, greenish-yellow, drupaceous with 2 pyrenes, the seeds with a straight embryo. TYPE AND SOLE SPECIES: *Ceratiola ericoides* Michx. (*C. falcatula* Gandoger, *Empetrum aciculare* Bertol.) (Name from Greek *ceras*, horn, apparently alluding to the flabellate style-branches.) — ROSEMARY.

Often covering extensive areas, *Ceratiola* is associated with pines and oaks throughout its range from Florida to South Carolina and Mississippi, and is a more or less characteristic shrub of the *Pinus clausa*-scrub in Florida. It does not occur on the Florida Keys. In some areas, especially on coastal sand dunes, it is associated with a shrub of similar habit and stature, *Solidago* (*Chrysoma*) *pauciflosculosa* Michx. Inhabiting extremely dry situations in pinelands, in sand hammocks and on inland sand dunes, often in almost pure sand with *Selaginella arenicola* Underw. and *Cladonia*,

Ceratiola is often ravaged by fire. In southern Florida it may be seriously parasitized by the lauraceous woevine, *Cassytha filiformis* L.

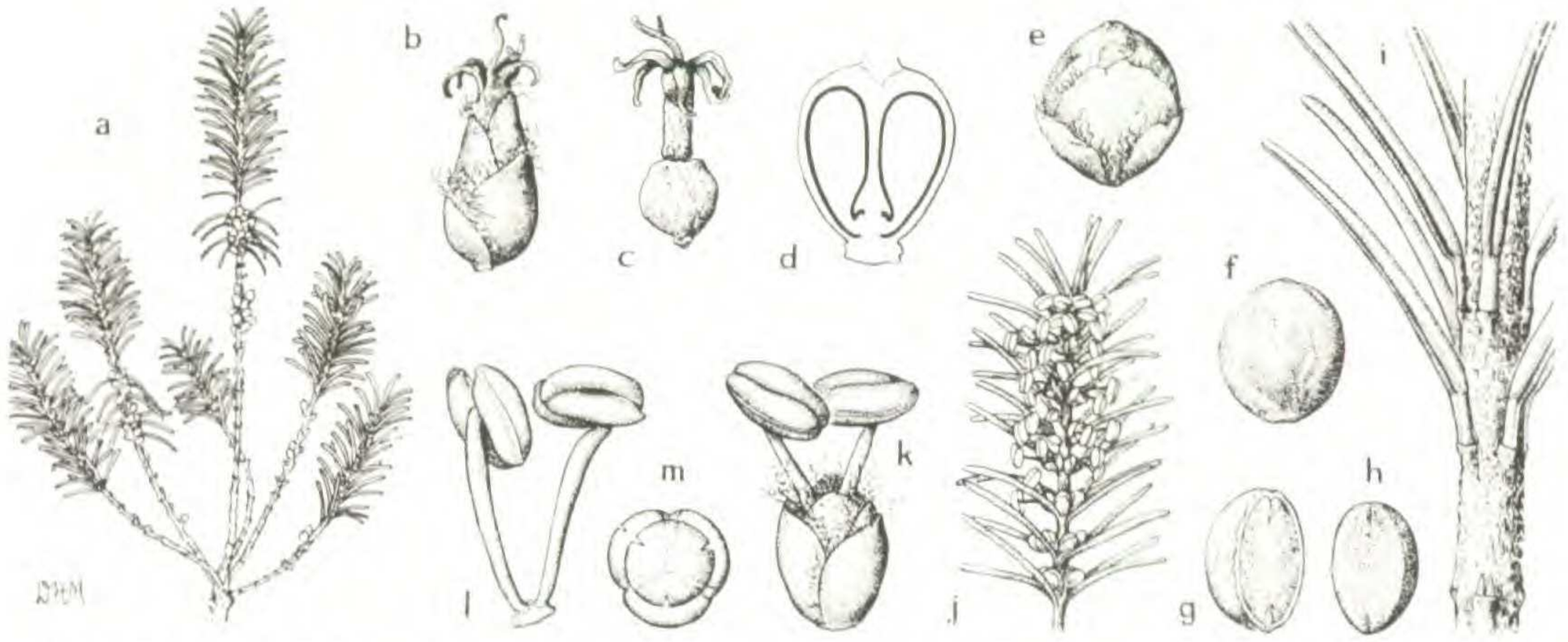

FIG. 1. **Ceratiola.** a–m, *C. ericoides*: a, habit, ♀ plant, × ½; b, ♀ flower, × 6; c, pistil, × 6; d, young ovary, semi-diagrammatic vertical section, showing two locules each with a single ascending ovule, × 12; e, mature fruit inclosed in weathered bracts and sepals, × 6; f, mature fruit free of bracts and sepals, × 6; g, pyrene inclosed in ovary wall, × 6; h, pyrene, × 6; i, portion of vegetative shoot showing position and arrangement of leaves — note articulate, pulvinate, appressed petioles, × 6; j, portion of ♂ shoot in flower, × 1; k, ♂ flower, × 6; l, stamens of a single ♂ flower, × 6; m, pollen tetrad, ca. 30 μ diameter, × ca. 300.

Usually a well-formed shrub, *Ceratiola* is very exacting in habitat and, like *Empetrum* and *Corema*, is difficult to cultivate, presumably because of a mycorrhizal relationship. The common name rosemary refers to the superficial resemblance to *Rosmarinus officinalis* L.

Little is known concerning the agent of pollination (wind?), germination and other biological features of the species.

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DIAPENSIACEAE (DIAPENSIA FAMILY) [3]

Low, evergreen herbs or subshrubs of acid soils, tufted or creeping, with simple exstipulate, alternate leaves. Flowers regular, the sepals 5, free, imbricate, the petals 5, separate or united, the corolla campanulate or funnel-shaped. Androecium typically of two whorls: an outer of 5 connivent fertile stamens, and an inner (when present) of 5 staminodia oppo-

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site the petals; filaments adherent to the petals (and sometimes monadelphous, as well); pollen grains single, 3-colporate. Style simple, the stigma 3-lobed, the ovary 3-loculed, superior, lacking a disc at the base; ovules 2-integumented, the placentation axile. Fruit a loculicidal capsule; seeds as in Ericaceae. (Including Galacaceae of Small's Manual.)

A small family of five genera, primarily of eastern America and eastern Asia (with the exception of the circumpolar *Diapensia lapponica* L.), forming a natural group with numerous reticulate relationships. Two tribes, DIAPENSIEAE Gray and GALACINEAE Gray, generally are recognized, although variously delimited (see Gray, Drude, Diels).

The group is usually agreed to be related to the Ericales but differs from most in the simple pollen grains, the epipetalous stamens and the absence of a disc. In view of the importance accorded embryological evidence in allying the Empetraceae with the Ericales it should be noted that the embryological features of *Diapensia lapponica* do not fit with those of other members of the Ericales. Further embryological studies of other genera are highly desirable. The family is currently placed either with the Ericales or in a separate order Diapensiales. Chromosome structure and basic number are similar throughout those members of the family thus far examined. The stamens and staminodia present interesting problems in function and morphology.

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KEY TO THE GENERA OF DIAPENSIACEAE

A. Plant with small awl-like leaves; prostrate, creeping; staminodia lacking; anthers 2-locular, apparently transversely dehiscent, each locule awned on the lower side; capsule with a persistent but easily broken columella. . . . . 1. *Pyxidanthera*.

A. Plant rhizomatous with shining oval to orbicular leaves; 5 staminodia present.
  B. Flowers large, solitary; petals connate, crenate-undulate-toothed; anthers large, oval, 2-locular; staminodia distinct, near base of corolla; capsule with a persistent columella; seeds ovoid or spherical. . . . . 2. *Shortia*.

B. Flowers small, numerous, in wand-like racemes on naked scapes; petals entire, distinct; stamens and staminodia monadelphous, forming a tube adnate to the petals; anthers 1-locular; capsule without a columella; seeds angular. ..... *3. Galax.*

1. **Pyxidanthera** Michx. Fl. Bor.-Am. 1: 152. *pl. 17.* 1803.

Creeping, prostrate, evergreen subshrub from a woody root, the small leaves alternate, oblanceolate, awl-pointed, sessile and hairy on the upper side (at least near the base). Flowers solitary and sessile on short, densely leafy branches. Sepals concave, oblong, reddish. Corolla white, about 5–10 mm. broad, the petals united by the broad stamen-filaments to form a tube, the lobes broadly spatulate, cuneate or obovate-cuneate. Stamens alternating with the petals, the filaments white, almost petal-like, the anthers bent inward; anther locules 2, each apparently dehiscing transversely and awned at the base; staminodia lacking. Style as long as the corolla tube, increasing somewhat in length in age; ovules 4–6 in each locule of ovary. Fruit with a persistent but brittle and easily broken columella; seeds globular, regularly pitted (seldom collected). $2n = 12$. TYPE SPECIES: *P. barbulata* Michx. (Name from the Greek *pyxis*, a small box, and New Latin *anthera*, for anther, from the appearance and dehiscence of the anthers.) — PIXIE, FLOWERING-MOSS.

One or two species: *Pyxidanthera barbulata*, of sandy pine barrens, usually seasonally wet, on the coastal plain from New Jersey to Virginia, and North and South Carolina, and *P. brevifolia* Wells, of the inner coastal plain, Harnett Co., N. C. to Darlington Co., S. C. The status of this second species, which is associated with *Quercus laevis* Walt. and *Pinus australis* Michx. f. on the rolling sand hills, needs careful study, for it appears to intergrade in moister habitats with the more widespread plant. Although *P. brevifolia* when well developed is characteristic in aspect, its only distinctive features are the smaller size of all parts and the greater hairiness of the leaves and stems, characteristics which may well be attributable to the more xeric habitat and which are matched or approached by various smaller specimens from New Jersey and North Carolina.

The mechanical operation of the awned, connivent anthers, which are apparently transversely dehiscent, is probably significant in the biology of the small, white flowers which are borne abundantly in March and April. Pollen is not discharged from the anther unless the awned tip is pushed downward. A comparison with the stamens of *Diapensia* suggests that the orientation of the anther-locules has changed from vertical to horizontal in the inwardly bent anthers of this plant so that the dehiscence is not truly "transverse."

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2. **Shortia** Torrey & Gray, Am. Jour. Sci. Arts I. **42:** 48. 1842; II. **45:** 402. 1868, nom. cons.

Low, evergreen, perennial herb, forming dense clumps or carpets, the foliage combining the aspect of *Galax* and *Pyrola*. Plants spreading by horizontal rhizomes bearing clustered long-petioled, broadly elliptic to sub-orbicular truncate-emarginate, cordate, lustrous leaves, toothed along the margin, and much smaller leaves or scales. Flowers 2–3 cm. high, solitary on bracted peduncles, nodding. Sepals ovate, imbricate. Corolla open-campanulate, white, pale pink or pale blue, the petals united, the lobes undulate-crenate notched. Fertile stamens with conspicuous, 2-loculed anthers bent sharply inward and connivent in the tube; staminodia borne near the base of the corolla and incurving over the ovary. Style elongate; capsule globular, 3-valved and with a persistent columella bearing the globular or ovoid seeds. $2n = 12$. (*Sherwoodia* House; not *Shortia* Raf., 1840, nom. rejic.) TYPE SPECIES: *Shortia galacifolia* Torrey & Gray. (Dedicated to Charles Wilkens Short, 1794–1863, of Kentucky, "whose attainments and eminent services in North American botany are well known and appreciated both at home and abroad.") — SHORTIA, OCONEE-BELLS, LITTLE COLTSFOOT.

In North America a single species and in Japan, Formosa and China perhaps 9–11 species, depending upon specific and generic concepts. *Shortia galacifolia*, *S. uniflora* Maxim., of Japan, and *S. sinensis* Hemsl. form a closely related group of species with solitary flowers and staminodia. Other species with several-flowered inflorescences and partially developed, although sterile, stamens have been treated as the genus *Schizocodon* Sieb. & Zucc., while four species described from Formosa with several-flowered inflorescences and no staminodia would be placed in *Shortiopsis* Hayata. All of these species appear to be closely related, however, and are best treated as a single genus, *Shortia*. The nearest ally is the Sino-Himalayan *Berneuxia* Decne.

Shortia galacifolia, a handsome plant with an intriguing history shares in our area the special fame of *Franklinia* and "Bartram's Ixia" (*Spheno-stigma coelestinum* (Bartr.) R. C. Foster). Collected by André Michaux in the Carolina mountains in 1787, the specimen was seen by Asa Gray in Paris in 1839 and was later described as a new genus. All searches for the plant were futile, but a second species described from Japan was recognized by Gray as belonging to the genus. *Shortia galacifolia* finally was rediscovered by George M. Hyams, in McDowell Co., N. C., in 1877, and, in 1886, was found by Sargent and Boynton near the junction of the Horsepasture and Toxaway Rivers in Oconee Co., S. C.

The plant is now known from two limited areas some 60 miles apart: var. *galacifolia*, primarily in the drainage of the Keowee River in Oconee and Pickens counties, S. C., Rabun Co., Ga., and Transylvania Co., N. C., and var. *brevistyla* P. A. Davies, in McDowell and Burke counties, N. C.

FIG. 2. DIAPENSIACEAE. a–h, **Shortia.** *S. galacifolia*: a, habit, × ¼; b, flower, × 1; c, lateral view of flower, corolla removed to show calyx and bracts, × 1; d, opened corolla, × 1; e, stamen, lateral view, × 4; f, staminodium, × 6; g, ovary, vertical section, semi-diagrammatic, × 4; h, ovary, cross section, × 4. i–q, **Pyxidanthera.** i–p, *P. barbulata*: i, habit, branchlet from above, × 1; j, flower, × 4; k, tip of flowering branchlet with flower after fall of corolla, × 4; l, opened corolla, × 4; m, stamens, × 10; n, immature fruit with calyx (2 lobes removed), × 4; o, ovary, cross section, × 10; p, seed, × 20. q, *P. brevifolia*: opened capsule from above, showing persistent but easily dislodged columella in

The two varieties differ in petal-length, -notching and -venation, length of staminodial hairs and length of styles. The ratio of length of style to length of mature ovary is 1:2.4 in the Keowee area and 1:1.3 in McDowell County. On this and other bases it appears that Michaux' specimen came from near the spot where Sargent and Boynton first found it.

Shortia is still abundant in a part of the Keowee area but should be protected from vandalism and excessive commercialism. It occurs in moderately acid soils with good aeration and usually with abundant moisture, growing best under *Rhododendron maximum* or *Tsuga*, but often in association with *Pinus Strobus*, *P. rigida*, *Liriodendron*, *Liquidambar* and *Kalmia latifolia* and various other Ericaceae. The altitudinal range is from about 600 feet (180 m.) to well above 1600 feet (500 m.) but the plant is hardy far to the north of its restricted range. The proterogynous flowers are borne in March and early April and the seeds mature from late April to May (or June). It has been suggested that the restricted distribution is related to the lack of a dispersal mechanism and to limited reproduction by seeds, for the seeds often germinate even within the capsule. However, natural reproduction by seeds is reported in Amherst Co., Virginia, and in the Keowee region.

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center, × 4. r–x, **Galax.** *G. aphylla*: r, habit, × ¼; s, flower, from above, × 4; t, opened corolla and staminal tube, × 4; u, stamen and anther, × 10; v, ovary with 3 sepals and bracteole, × 5; w, fruit, × 4; x, seed, × 20.

3. **Galax** L. Sp. Pl. 1: 200. 1753, partim, emend. Nutt. Gen. 1: 145. 1818, nom. cons.

Low herbs with scaly-bracted rhizomes forming a thick, matted tuft bearing long-petioled, round-cordate, crenate-toothed, lustrous evergreen leaves, the plant spreading by slender cord-like rhizomes which later become branched, thickened, and leaf-bearing at the tips. Flowers small (4–5 mm.), white, each with minute bracts at the base, borne in a wand-like raceme on a slender, naked scape in May (or July at higher altitudes). Sepals 1/3–1/2 the length of the oblong-spatulate petals. Petals distinct to the base, nearly erect or spreading. Filaments of 5 fertile stamens and 5 staminodia united, forming a tube adnate to the petals at the base, falling with the petals; free tips of the staminodia fleshy, nearly erect, the fertile anthers bent at right angles to the tube, connivent, each anther apparently 1-loculed and opening horizontally (actually across the top), the lower (inner) half tapering to an obtuse point. Pistil about as long as the calyx, the style short, the stigma 3-lobed. Capsule obpyriform, about 3 mm. long, without a columella, the seeds numerous, small, brown, angular, tapering, with a cellular seed coat. $2n = 12, 24$. (Not *Galax* L., 1754, nom. rejic.) TYPE AND SOLE SPECIES: *G. aphylla* L. (Name from Greek, *gala*, milk, presumably from the white flowers.) — GALAX, GALAXY, WAND-FLOWER, COLTSFOOT, BEETLEWEED, BEETLE-PLANT, SKUNK-CABBAGE.

A handsome and distinctive monotypic genus ranging from northern West Virginia and northwestern Maryland to the coastal plain of eastern Virginia and eastern North Carolina, to central Georgia, central Alabama and central Tennessee, in acid soils, generally in mesophytic associations with *Kalmia* or *Rhododendron* and other Ericaceae. The plant reaches its best development in rich, acid, humus-covered soils in the piedmont and Blue Ridge where, from North Carolina to Georgia, great quantities of the leaves, which become bronzed in winter, are gathered and sold to florists.

Galax provides one of the clearest, simplest and best studied cases of autoploidy in wild populations. Diploids occur throughout the range of the species, except in the Virginia coastal plain, where only the tetraploids are known. Tetraploid plants grow in the same habitats and areas as diploids, but are especially concentrated in the region from southern Virginia through the North Carolina mountains into South Carolina and Georgia. They appear to be absent from the northern and western parts of the range. Under the most favorable conditions the leaves of tetraploids may reach 15 cm. wide, while those of diploids attain only 10 cm. The plants are usually indistinguishable in the field, however, and no morphological distinctions other than those of size are known. No triploids and no meiotic irregularities have been reported in either diploids or tetraploids.

The apparently one-loculed anthers are strongly reminiscent of those of *Pyxidanthera* and suggest a similar mode of development. The flowers are most like those of *Pyxidanthera* (except for the presence of staminodia)

but in vegetative features *Galax* suggests *Shortia*. The genus has been treated either as the sole member of the tribe GALACINEAE or has been placed there with *Shortia* and *Berneuxia*.

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